

BIODIVERSITY
REVIEW


Reproductive biology of Australian acacias: important mediator of invasiveness?

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ABSTRACT

Aim Reproductive traits are important mediators of establishment and spread of introduced species, both directly and through interactions with other life-history traits and extrinsic factors. We identify features of the reproductive biology of Australian acacias associated with invasiveness.

Location Global.

Methods We reviewed the pollination biology, seed biology and alternative modes of reproduction of Australian acacias using primary literature, online searches and unpublished data. We used comparative analyses incorporating an *Acacia* phylogeny to test for associations between invasiveness and eight reproductive traits in a group of introduced and invasive (23) and non-invasive (129) species. We also explore the distribution of groups of trait 'syndromes' between invasive and non-invasive species.

Results Reproductive trait data were only available for 126 of 152 introduced species in our data set, representing 23/23 invasive and 103/129 non-invasive species. These data suggest that invasives reach reproductive maturity earlier (10/13 within 2 years vs. 7/26 for non-invasives) and are more commonly able to resprout (11/21 vs. 13/54), although only time to reproductive maturity was significant when phylogenetic relationships were controlled for. Our qualitative survey of the literature suggests that invasive species in general tend to have generalist pollination systems, prolific seed production, efficient seed dispersal and the accumulation of large and persistent seed banks that often have fire-, heat- or disturbance-triggered germination cues.

Conclusions Invasive species respond quicker to disturbance than non-invasive taxa. Traits found to be significant in our study require more in-depth analysis involving data for a broader array of species given how little is known of the reproductive biology of so many taxa in this species-rich genus. Sets of reproductive traits characteristic of invasive species and a general ability to reproduce effectively in new locations are widespread in Australian acacias. Unless there is substantial evidence to the contrary, care should be taken with all introductions.

Keywords

Biological invasions, breeding system, invasive alien species, pollination, reproductive syndromes, reproductive traits, seed dispersal

INTRODUCTION

A predictive understanding of invasiveness is needed to manage existing invasive species and for objective screening of new introductions. Elucidating the determinants of invasiveness and understanding how these interact with environmental features and extrinsic factors to mediate invasion success are fundamental questions in invasion ecology (Richardson & Pyšek, 2006). Anthropogenic and environmental factors and various life-history traits, particularly features associated with reproduction and dispersal (Rejmánek *et al.*, 2005; Thuiller *et al.*, 2006; Pyšek & Richardson, 2007), are often associated with invasion success (or lack thereof). Previous studies comparing life-history traits of invasive species have found several reproductive traits including seed mass, fecundity (number of seeds produced), dispersal mode and dispersal ability to be important for overcoming barriers to invasion in a new environment (Hamilton *et al.*, 2005; Pyšek & Richardson, 2007; Moravcová *et al.*, 2010; Castro-Díez *et al.*, 2011). There has, however, been no comprehensive analysis of the roles of such traits in invasiveness in Australian acacias, a speciose group of plants containing several invasive species.

This study assesses the current state of knowledge regarding associations between reproductive traits and invasiveness in this group, which here refers to the *ca.*1012 taxa in the genus *Acacia* (hereafter referred to as 'Australian acacias' or *Acacia*, formerly placed in *Acacia* subgenus *Phyllodineae* and synonymous with *Racosperma*) that have Australia as at least part of their native range; see Miller *et al.* (2011) for a more recent phylogenetic treatment of this and related groups. To do this, we present an analysis in two parts: (1) a quantitative comparative analysis of specific reproductive traits for which appropriate data were available; and (2) a qualitative literature review of reproductive traits for which we could not find quantitative data, but which may be important in predicting invasiveness. We conclude with the implications for management.

Australian acacias are an excellent group for exploring determinants of invasiveness and are likely to become a model system against which other invasive plant groups are compared (Richardson *et al.*, 2011). They comprise a phylogenetically and geographically distinct group (natural distributions virtually confined to the Australian continental landmass) with 1012 described species (Richardson *et al.*, 2011), of which at least a third have been introduced and 23 are invasive in different parts of the world (Richardson & Rejmánek, 2011; Richardson *et al.*, 2011). Their well-documented introduction histories (e.g. Le Roux *et al.*, 2011) and records of invasiveness in different introduced ranges make comparative studies possible on continental and global scales. Australian acacias appear to possess a suite of reproductive and other life-history traits that have been suggested as instrumental in their success as invasive species (Milton & Hall, 1981; Richardson & Kluge, 2008). Unfortunately, invasive taxa among Australian acacias are far better studied than are non-invasive taxa; this is in line

with a general bias in invasion ecology whereby invasive species that exert greater impacts on invaded environment are better studied (Pyšek *et al.*, 2008). This complicates statistical analysis of associations between species character traits and invasiveness.

Little is known in general about such associations (Gallagher *et al.*, 2011), and to date, no multi-species, multi-regional study has explored how reproductive traits influence invasiveness of Australian acacias. In this study, we review available published and unpublished information on their reproductive traits and trait 'syndromes' (sets of reproductive traits that repeatedly favour a particular group of pollinators, method of reproduction, agent of seed dispersal or germination system) and compare trait values between (1) rare and common Australian acacias; (2) invasive Australian species in their native and introduced ranges; and (3) introduced invasive species and introduced non-invasive Australian acacias. Our aim is to identify those traits associated with invasiveness. Our approach has been dictated by the availability of data. For those traits for which data are available (Table S1), we use phylogenetically controlled comparative analyses to ask which reproductive traits, alone or in combination, are significant correlates of invasiveness. For those traits we were unable to analyse quantitatively, we qualitatively review all available information to address the questions: (1) Are there distinct reproductive syndromes that differ between invasive and non-invasive species? and (2) does pollinator-mediated seed production reduce or enhance naturalization or invasion in any regions? Such an approach has the potential to yield insights that are of value to plant invasion ecology in general and for refining screening protocols (e.g. Gordon *et al.*, 2010) for assessing the risk of further introductions of *Acacia* species that may lead to invasions.

Methods

Species list

We used the classification scheme of Richardson & Rejmánek (2011) to define which species are considered invasive ($n = 23$). The objective criteria used in their study (following Pyšek *et al.*, 2004) are more conservative than those applied by others (e.g. Randall, 2002), and only species that have spread considerable distances from parent populations are considered 'invasive'. However, the criteria are not as strict as in other studies, such as Castro-Díez *et al.* (2011), who regarded species as 'invasive' (sensu Pyšek *et al.*, 2004) only when supported by at least two different sources of information from different countries. Species were defined as having been introduced ($n = 152$) only if a herbarium record for that species has been collected from outside Australia (Richardson *et al.*, 2011).

We compiled data on at least one of eight reproductive traits for 450 of the 1012 species in the Australian *Acacia* group. Of the 860 non-introduced species, data were available for six of the traits for 324 species (Table S2). Of the 152 introduced species, data were available for all eight traits for 126 species

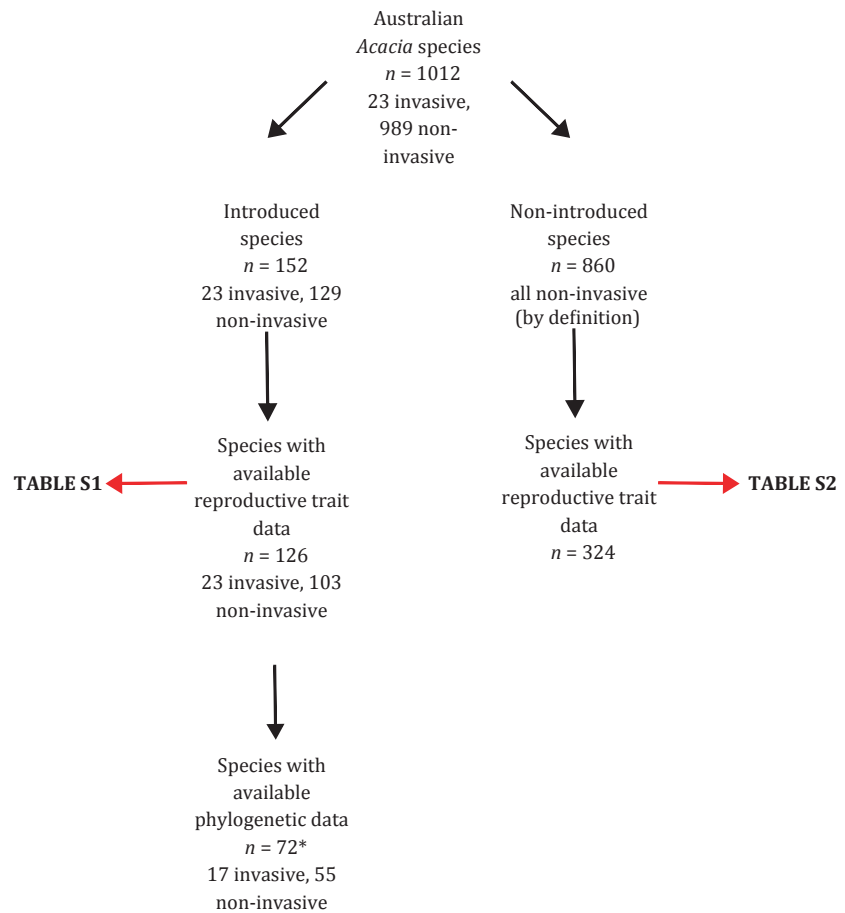


Figure 1 Breakdown of Australian *Acacia* species used in this study. *One of the species for which there was phylogenetic data had no available reproductive trait data.

(23 invasive, 103 non-invasive; see Table S1) – see Fig. 1 for a breakdown of species used in this study. We analysed data on reproductive traits using only introduced species to reduce biases caused during the introduction process.

Statistical analysis

We used R for all statistical analyses (R Development Core Team, 2011). Reproductive traits were used as explanatory variables, and invasive status (invasive and non-invasive) was used as the response variable. Explanatory variables used in quantitative analyses comprised: time to reproductive maturity; index of self-incompatibility (ISI) (number of infructescences/inflorescence); ISI (number of pods/inflorescence); combined measure of breeding system; dispersal agent (ant- or bird-dispersed seed); seed mass; resprouting ability; and length of flowering period (see Appendix 1 for details and references). Seed mass was log transformed to reduce skewness in the data. Seeds were considered to be dispersed by birds either if this was conclusively reported in the literature or, based on seed morphological traits, if the arils/funicles or elaiosomes were specifically described as being orange, yellow or red. Species were considered to be ‘not bird dispersed’ if they were reported to be dispersed by ants in the literature and

where dispersal by birds was not mentioned. Species for which clear data were not available were omitted from the analysis. A combined measure of breeding system was inferred from multi-locus outcrossing rate (t_m), both ISI measurements, and breeding system (t_m and breeding system not used in final analyses; see Appendix 1 and Table S1). We considered a species as outcrossing if $t_m \geq 0.8$ or $ISI \leq 0.5$; otherwise, species were considered to have mixed mating systems.

Because species do not represent independent data points in comparative studies (Hadfield & Nakagawa, 2010; Stone *et al.*, 2011), we incorporated phylogenetic relationships among sampled species into our analyses using a generalized least-squares (gls) framework in the nlme package (Pinheiro *et al.*, 2009). This approach assumes a Brownian model of character evolution in which trait covariance between a pair of species decreases linearly since their time of divergence from a shared common ancestor. The phylogenetic relationship between taxa was inferred using Bayesian methods incorporated in the software MrBayes version 3.1.2 (Ronquist & Huelsenbeck, 2003). Our analysis incorporates sequence data for two nuclear genes (nuclear ribosomal DNA internal (ITS) and external (ETS) transcribed spacers) and four chloroplast regions (*psbA-trnH* intergenic spacer, *trnL-F* intron and intergenic spacer, *rpl32-trnL* intergenic spacer and a portion of the *matK*

introns), comprising a tandem alignment of 5912 base pairs. Contiguous sequences were edited using Sequencher™ v.3.0 (Gene Codes Corporation) and manually aligned in BioEdit sequence alignment editor v.4.8.6 (Hall, 1999). Appropriate models of molecular evolution for implementation in MrBayes were identified using the programme Modeltest v.1.1 (Posada & Crandall, 1998), which identified the GTR + I + G model (general time reversible model incorporating a proportion of invariant sites and gamma-distributed rate variation in variable sites) for both the plastid and nuclear partitions of our data set. The Markov chain Monte Carlo search in MrBayes was run for two million generations with trees sampled every 1000 generations. MrBayes performed two simultaneous analyses starting from different random trees (Nruns = 2), each with four Markov chains (Nchains = 4). The first 200 sampled trees were discarded from each run as burn-in. We used the 50% majority rule consensus phylogram as our working phylogeny, with node support expressed in terms of posterior probability values. All trees were rooted using *Pararchidendron pruinosum* as an outgroup taxon.

The resultant phylogeny incorporated 72 species of the 126 species (see Miller *et al.*, 2011), and only data for these species were incorporated into phylogenetically controlled analyses (17 invasive, 55 non-invasive; see Fig. 2 for phylogenetic tree and Appendix S1 for species accession numbers). Because our analytical approach to determine phylogenetic independence requires a fully resolved phylogeny, polytomies were broken by inserting very small non-zero branch lengths. Reanalysis with such instances pruned from the data gave near-identical results (not shown). To assess the impact of phylogenetic patterns in our trait data, we compared analyses incorporating phylogenetic information for this subset of 72 species with phylogeny-free analyses for the same species set. To illustrate patterns in the full data set, we also carried out phylogeny-free analyses across the full set of 126 species. For both data sets ($n = 72$ and $n = 126$), phylogeny-free tests of trait differences between invasive and non-invasive species involved Pearson's chi-square tests for binary explanatory variables and generalized linear models for individual continuous explanatory variables.

Results

Of the eight reproductive traits we assessed, only two showed significant differences between invasive and non-invasive species in phylogeny-free analyses (Table 1A,B; see Appendix S2 for actual parameter estimates, results were similar when using either all 126 species or the subset of 72 species for which we have a phylogeny). The proportion of species that reach reproductive maturity within two years was significantly higher for invasive acacias ($\chi^2 = 6.90$, d.f. = 1, $P = 0.009$). Invasive species also had a significantly higher probability of being resprouters ($\chi^2 = 4.34$, d.f. = 1, $P = 0.037$) than non-invasive species. Incorporation of phylogenetic relationships into the analysis for 72 species removed the significance of resprout ability, but supported our results from the phylogeny-free analyses that invasive species reach reproductive maturity

earlier (gls: coefficient = -0.553 , $t = -3.18$, $P = 0.004$; Table 1B, Appendix S3).

LITERATURE REVIEW: REPRODUCTIVE BIOLOGY OF AUSTRALIAN ACACIAS

Pollination biology

As a broad generalization, we expect successful invasive species to share at least some of the following floral traits (Baker, 1955; Chittka & Schürkens, 2001; Brown *et al.*, 2002; Ghazoul, 2002; Gross *et al.*, 2010):

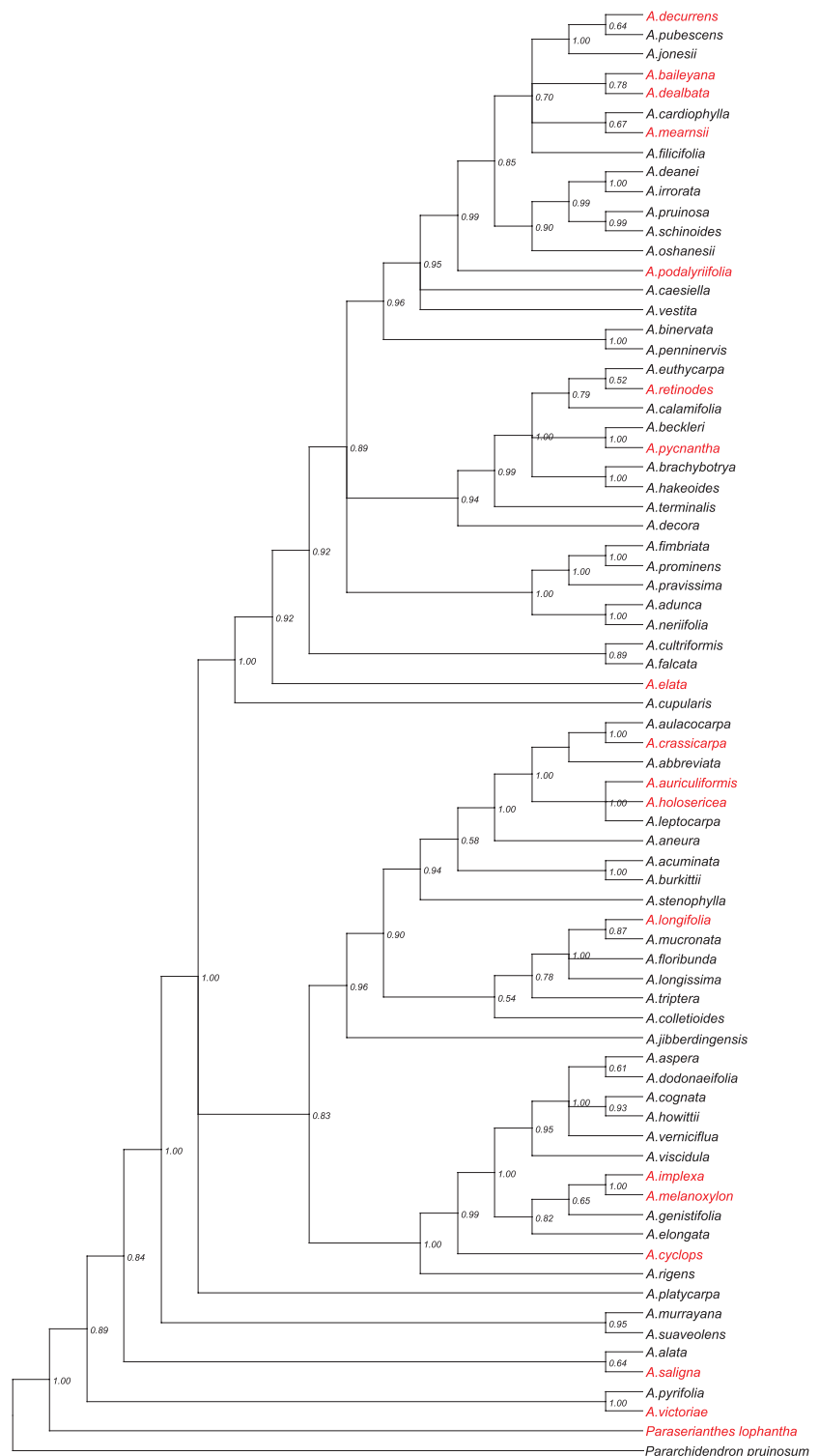
1. High attractiveness to available flower visitors and floral morphologies allowing pollination by many different organisms.
2. Production of very large numbers of long-lived flowers allowing seed-set even when visitation rates are low; and/or an ability to self-pollinate or reproduce vegetatively.
3. Floral induction cues match those triggering flowering in native species and emergence of native flower visitors.

Worldwide, taxa classified in the polyphyletic group *Acacia sensu lato* (genera *Acaciella*, *Mariosousa*, *Senegalia*, *Vachellia*; McNeill *et al.*, 2006) share many of these morphological traits but differ in their global distributions, pollinator assemblages and specific aspects of floral biology (Stone *et al.*, 2003). All have small tubular flowers collected together into spherical or elongated flower heads, with pollen presented on the inflorescence surface (Stone *et al.*, 2003; Raine *et al.*, 2007). Clustering of the pollen grains into a composite unit, termed a 'polyad', is a key component of the pollination efficiency of all acacias, providing an efficient means of dispersal via pollinators (Kenrick & Knox, 1982). There are always fewer ovules per ovary than pollen grains per polyad, so one polyad from a single pollination event can potentially fertilize all the ovules (Kenrick & Knox, 1982). The stigmas of the flowers are also distributed over the surface of the flower heads and are freely accessible, so that any insect that travels from one tree to another is a potential pollinator. Recruitment of insects is often enhanced by the release of floral scent just before pollen release, and visual advertisement is often maximized by synchronized opening of flowers, both within a single tree and often within a local species' population (Stone *et al.*, 2003). Floral morphology is a conserved trait across the genus and does not distinguish invasive from non-invasive Australian acacias. Such generalized morphology may facilitate invasion as it reduces the risk of pollinator limitation for introduced plants (Richardson *et al.*, 2000a). See Fig. 3 for photographs of pollination biology traits associated with invasiveness in Australian acacias.

Floral biology

The fundamental floral morphology shared by all Australian acacias identifies a generalist entomophilous pollination syndrome as it provides accessible floral rewards to almost any insect visitor (Bernhardt, 1989). A second pollination

Figure 2 Bayesian phylogenetic tree depicting relationships among taxa included in the phylogenetic generalized least-squares analysis. Numbers at nodes indicate the Bayesian posterior probability (PP). Invasive taxa are shown in red. *No reproductive trait data were available for *A. vestita*.



syndrome involves pollination by nectar-feeding birds and is associated with the location of a large extrafloral nectary near the inflorescence. Pollen collected on the bird's head is transferred while it feeds on the gland's nectar (Knox *et al.*, 1985). Some species display both insect and bird pollination syndromes (e.g. *A. terminalis*, Kenrick *et al.*, 1987). As with morphology, having a generalized pollination system reduces

pollinator limitation of seed set and is thus likely to contribute to the invasive success of Australian acacias (Richardson *et al.*, 2000a).

Australian acacias show two features in their floral biology that together distinguish them from all other related taxa (Stone *et al.*, 2003). First, no Australian acacias are recorded to secrete floral nectar, although some produce extrafloral nectar

Table 1A Phylogeny-free analyses of correlations between reproductive traits and invasiveness of 126 introduced Australian *Acacia* species (23 invasive/103 non-invasive Table S1).

Explanatory variables	Response variables		Test	Relationship
Reproductive traits	Invasive	Not invasive		
<i>Continuous</i>	Summary (<i>n</i> ; mean, μ ; range)			
Index of self-incompatibility (ISI) (infructescence/inflorescence)	<i>n</i> = 6 μ = 0.425 range = 0.02–0.86	<i>n</i> = 3 μ = 0.42 range = 0.13–0.96	GLM (negative binomial errors): $z = 0.010$, $P = 0.992$	No effect No effect
ISI (pods/inflorescence)	<i>n</i> = 7 μ = 0.339 range = 0.008–0.79	<i>n</i> = 3 μ = 0.447 range = 0.07–1.1	GLM (negative binomial errors): $z = -0.212$, $P = 0.832$	No effect No effect
Seed mass (mg)	<i>n</i> = 23 μ = 20.3 range = 5.7–47.8	<i>n</i> = 99 μ = 21.1 range = 2.72–219	GLM (binomial errors; response var. log10 transformed): $z = 1.14$, $P = 0.254$	No effect No effect
Length of flowering (months)	<i>n</i> = 22 μ = 4.909 range = 2–10	<i>n</i> = 59 μ = 4.890 range = 2–12	GLM (binomial errors): $z = 0.042$, $P = 0.966$	No effect No effect
<i>Binary</i>	Summary ((<i>n</i> , number of total for each factor level); mean, μ ; confidence interval (CI; 97.5%))			
Time to reproductive maturity (>2 years or <2 years)	<i>n</i> = 13 (10 < 2 years, 3 > 2 years) μ = 77% <2 years CI = 54–100%	<i>n</i> = 26 (7, <2 years, 19, >2 years) μ = 27% <2 years CI = 12–46%	Chi-square: $\chi^2 = 6.90$, d.f. = 1, $P = 0.0086$	Invasive species reach reproductive maturity earlier than non-invasive species
Combined measure of breeding system ('mixed' or 'outcrossing')	<i>n</i> = 10 (2 mixed, 8 outcross) μ = 20% mixed CI = 0–50%	<i>n</i> = 3 (1 mixed, 2 outcross) μ = 50% mixed CI = 0–100%	Chi-square: $\chi^2 = 0.0903$, d.f. = 1, $P = 0.764$	No effect
Seed dispersal ('bird' or 'not bird')	<i>n</i> = 15 (8 bird, 7 not bird) μ = 53% bird CI = 27–80%	<i>n</i> = 12 (4 bird, 8 not bird) μ = 33% bird CI = 8–58%	Chi-square: $\chi^2 = 0.422$, d.f. = 1, $P = 0.516$	No effect
Ability to resprout (True/False)	<i>n</i> = 21 (11 can resprout, 10 cannot) μ = 52% CI = 33–71%	<i>n</i> = 54 (13 can resprout, 41 cannot) μ = 24% CI = 13–35%	Chi-square: $\chi^2 = 4.34$, d.f. = 1, $P = 0.037$	Ability to resprout significantly positively related to species being invasive

Details of actual parameter estimates are given in Appendix S2.

to attract insect and bird pollinators (Knox *et al.*, 1985; Vanstone & Paton, 1988). There are also other acacia (*Acacia* s.l.) species that lack nectar, including *A. nilotica* (Stone *et al.*, 1998) – the most invasive African acacia in Australia (Radford *et al.*, 2002). A second distinctive feature is that individual flowers and flower heads are relatively long-lived in Australian acacias (Prescott, 2005) compared with other acacias. Flowers on a single flower head open over a series of days, and each flower head can last for up to two weeks (Stone *et al.*, 2003; George *et al.*, 2009). Intuitively, floral longevity should contribute to the success of Australian acacias as invaders, because long-lived flowers are tolerant of competition and have a

higher probability of pollination when pollination events are rare because of pollinator or mate limitation.

The ability of introduced Australian acacias to tolerate competition for pollination is likely to facilitate invasion, as introduced species enter an environment where all pollinators have established relationships with other plant species (Pyšek *et al.*, 2011). Flower heads of Australian acacias open gradually and asynchronously, which favours foraging by small bees that can gather resources in small packets (Stone *et al.*, 2003). *Acacia* flowers can be either male-only or hermaphrodite (Kenrick, 2003; George *et al.*, 2009). Australian *Acacia* species have strictly protogynous flowers where the stigma is receptive

Table 1B Comparison of phylogeny-controlled and phylogeny-free analyses of relationships between reproductive traits and invasiveness for 72 introduced Australian *Acacia* species (cf. 126 species in Table 1A), comprising 17 invasive and 55 non-invasive species.

Explanatory variables	Response variables			Phylogenetic generalized least squares	Relationship
Reproductive traits	Invasive	Not invasive	Test		
<i>Continuous</i>	Summary (<i>n</i> ; mean, μ ; range)				
ISI (Index of self-incompatibility) (infructescence/inflorescence)	<i>n</i> = 5 μ = 0.34 range = 0.02–0.78	<i>n</i> = 1 μ = 0.13 range = 0.13	GLM (binomial errors): $z = 0.522$, $P = 0.602$	$t = 0.107$, $P = 0.920$	No effect with or without phylogeny
ISI (pods/inflorescence)	<i>n</i> = 6 μ = 0.26 range = 0.008–0.77	<i>n</i> = 1 μ = 0.07 range = 0.07	GLM (binomial errors): $z = 0.475$, $P = 0.635$	$t = 0.139$, $P = 0.895$	No effect with or without phylogeny No effect with or without phylogeny
Seed mass (mg)	<i>n</i> = 17 μ = 20.34 range = 7.52–40.55	<i>n</i> = 53 μ = 23.16 range = 5.21–219.77	GLM (binomial errors); response var. log10 transformed): $z = 0.777$, $P = 0.437$	$t = 0.101$, $P = 0.315$	No effect with or without phylogeny No effect with or without phylogeny
Length of flowering (months)	<i>n</i> = 16 μ = 4.63 range = 2–10	<i>n</i> = 39 μ = 4.80 range = 2–12	GLM (binomial errors): $z = -0.330$, $P = 0.741$	$t = -0.077$, $P = 0.939$	No effect with or without phylogeny
<i>Binary</i>	Summary ((<i>n</i> , number of total for each factor level); mean, μ ; confidence interval (CI; 97.5%))				
Time to reproductive maturity	<i>n</i> = 10 (8 < 2 years, 2 > 2 years) μ = 75% <2 years CI = 50–100%	<i>n</i> = 16 (7, <2 years, 19, >2 years) μ = 48% <2 years CI = 19–69%	Chi-square: $\chi^2 = 5.44$, d.f. = 1, $P = 0.02$	$t = -3.18$, $P = 0.004$	Invasive species reach reproductive maturity earlier than non-invasive species with and without phylogeny
Combined measure of breeding system	<i>n</i> = 9 (1 mixed, 8 outcross) μ = 17% mixed CI = 0–33%	<i>n</i> = 1 (1 outcross) μ = 100% mixed CI = 100%	Chi-square: $\chi^2 = 1.98$, d.f. = 1, $P = 0.16$	$t = -0.103$, $P = 0.920$	No effect with or without phylogeny
Seed dispersal	<i>n</i> = 12 (6 bird, 6 not bird) μ = 49% bird CI = 23–75%	<i>n</i> = 5 (2 bird, 3 not bird) μ = 40% bird CI = 0–80%	Chi-square: $\chi^2 = 0.02$, d.f. = 1, $P = 0.88$	$t = -0.024$, $P = 0.981$	No effect with or without phylogeny
Ability to resprout	<i>n</i> = 15 (9 can resprout, 6 cannot) μ = 60% CI = 33–87%	<i>n</i> = 34 (7 can resprout, 27 cannot) μ = 23% CI = 9–35%	Chi-square: $\chi^2 = 5.67$, d.f. = 1, $P = 0.002$	$t = 1.08$, $P = 0.287$	Ability to resprout significantly positively related to species being invasive, but significance lost when phylogeny considered

Phylogenetic relationships among species were incorporated as a covariate in a generalized least-squares analysis (see Methods). Actual parameter estimates are given in Appendix S3.

before the anthers produce pollen (Stone *et al.*, 2003; George *et al.*, 2009). In contrast, the flower heads of African and American acacias are protandrous and release pollen synchronously, which makes them attractive to larger native bee species because all the resource is presented at once (Stone *et al.*, 2003; Raine *et al.*, 2007). To exploit this larger food

resource effectively, the larger African bees, which are important pollinators of African acacias, time their arrival at each species to coincide with its daily pollen release (Stone *et al.*, 1998). This foraging behaviour would be ineffective for the exploitation of Australian acacia flowers, and it is not surprising that the most prominent visitors to introduced

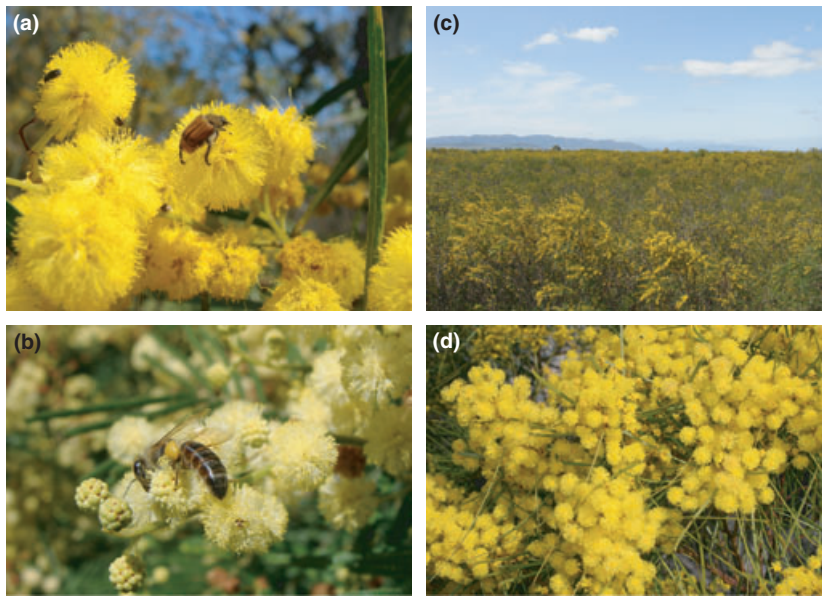


Figure 3 Important pollination biology traits associated with invasiveness in Australian acacias. These species share a generalist pollination syndrome as illustrated in South Africa where (a) *Acacia saligna* is being visited by native beetles (photograph: M.R. Gibson) and (b) *A. mearnsii* is being visited by the native honeybee, *Apis mellifera capensis* (photograph: A.M. Rogers). (c) Mass flowering in a field invaded by *A. saligna* in South Africa during its flowering peak in September (photograph: A.M. Rogers). (d) The dense flowers of *A. adunca* form an eye-catching, bright yellow floral display in Queensland (photograph: T. Low).

Australian acacias are often honeybees (*Apis mellifera*) (Bernhardt, 1987; Sedgley *et al.*, 1992; Sornsathapornkul & Owens, 1998; Alves & Marins-Corder, 2009), whose sensitivity to resource availability and ability to learn are both exceptional among bees (Willmer & Stone, 2004).

Other floral traits that may contribute to the invasive success of Australian acacias are precocity (early reproductive maturity) and longevity. Morgan *et al.* (2002) found that low final pod set (pods/inflorescence) in *A. baileyana*, as is seen in many acacias (Kenrick, 2003), was offset by precocious flowering and high flower numbers, which resulted in high seed production, probably partly facilitating its invasiveness. Early reproductive maturity is seen in many invasive acacias with some commencing flowering at just two years of age (see Table S1). In this study, both phylogeny-free and phylogenetic analyses suggested that short juvenile period was a significant factor distinguishing invasive acacias from non-invasive species. This result makes intuitive sense, because shorter juvenile periods enhance invasiveness by ensuring that seeds are produced sooner and thus confer an overall high seed production and allow for rapid accumulation of a soil seed bank. On a coarse level, floral biology appears essentially similar for all Australian acacias. Consequently, specific traits such as time of pollen release and inflorescence longevity are unlikely to distinguish invasive and non-invasive Australian acacias. However, subtle variations in combinations of sexual receptiveness and longevity (e.g. age-dependent floral colour variation; M.N. Prescott, unpublished data) could be important in this regard and require proper studies before being fully ruled out.

Pollination and pollen vectors

Pollinator assemblages vary on an annual, seasonal and geographic basis so that a diverse spectrum of floral foragers visit *Acacia* species in a given location, but the dominance of

specific vectors can vary inter- and intraspecifically (Bernhardt, 1989). In their native range, *Acacia* species are visited by a variety of flower foragers, but the most important pollinators are usually bees and wasps (*Apoidea*), followed by flies, beetles and birds (Kenrick *et al.*, 1987; Vanstone & Paton, 1988; Bernhardt, 1989; Stone *et al.*, 2003; Prescott, 2005). Social bees are relatively scarce in Australia, and most of the dominant native bees are small-bodied polylectic solitary species in the families Anthophoridae, Colletidae and Halictidae. The introduced honeybee is also an important and abundant pollinator of Australian acacias in both their native and introduced ranges (Bernhardt, 1987; Thorp & Sugden, 1990; Sedgley *et al.*, 1992; Prescott, 2005). Existing studies of introduced Australian acacias in South Africa show that native honeybees (*Apis mellifera capensis* and *A. mellifera scutellata*) are dominant pollen vectors followed to a lesser extent by flies and bees (M.R. Gibson, unpublished data; J.G. Rodger unpublished data) (see Table S3 for a comprehensive list of flower visitors). In other parts of the introduced range of Australian acacias, honeybees tend to be the most abundant and effective floral visitor in terms of visitation frequency and pollen-carrying load (Sornsathapornkul & Owens, 1998), although their distribution may be restricted to areas with sufficient availability of nectar flowers (Alves & Marins-Corder, 2009). Honeybees may be especially important for pollination in the context of *Acacia* invasions as they can learn to exploit new floral resources in a matter of hours (Willmer & Stone, 2004).

The importance of biotic pollination for reproductive success depends on whether abiotic pollination occurs. Although it remains to be tested and although pollen has been collected downwind of flowering *A. mearnsii* (Wattle Research Institute, 1952; Moncur *et al.*, 1989), *Acacia* inflorescences show no apparent adaptations for capture of wind-borne pollen. In contrast to typical wind-pollinated species, which have feathery stigmas and aerodynamic features that aid

in capture of pollen grains (Niklas, 1985, 1987), *Acacia* flowers have a very small cup-shaped stigma into which only one polyad can fit and lack any obvious aerodynamic structures. Wind-pollinated species have relatively high pollen to ovule ratios (median 22 150: 1) relative to animal-pollinated species (median 3450:1), although pollen-transfer efficiencies (proportion of removed pollen that is captured by stigmas) are similar (Friedman & Barrett, 2009). Typical of plants with aggregated (i.e. polyad-like) pollen (Harder & Johnson, 2008), the pollen to ovule ratio in *Acacia* is very low (53–360 for *A. mearnsii* based on measurements in Kenrick & Knox, 1982; Moncur *et al.*, 1991), compatible with dependence on animal pollen vectors. While it thus seems unlikely that wind pollination would make an appreciable contribution to fecundity, the possibility cannot yet be rejected. In the only test for wind pollination that we are aware of, fruit set of *A. mearnsii* was reduced but not eliminated in inflorescences enclosed in cages of wire and nylon mesh. However, bags reduced wind-borne pollen supply, and some flowers may have protruded through the cages and been pollinated by bees (Wattle Research Institute, 1952, 1961) so decisive experiments are still required to assess whether wind pollination is at all important for *Acacia*.

Because acacias are pollinated by generalist pollinators (such as the widely introduced honeybee), pollinator limitation seems an unlikely constraint to the spread of introduced Australian acacias relative to non-invasive taxa (Richardson *et al.*, 2000a) but this has not yet been studied. If pollination by *A. mellifera* enhances seed production of Australian acacias, then honeybees could facilitate *Acacia* invasions (and the facilitation could be reciprocal where both species are introduced, as in South America) (Barthell *et al.*, 2001; Morales & Aizen, 2002). We conclude that generalist pollination facilitates invasion, but there is no evidence to suggest that this factor alone explains the relative success of different Australian acacias as invasive and introduced non-invasive species both possess generalist pollination systems.

Phenology

Most Australian acacias tend to flower in massive displays from late winter to mid-spring (Bernhardt, 1989; Costermans, 2007) and have long-lived (and so competition tolerant) inflorescences (Stone *et al.*, 2003; Prescott, 2005), although the number of flower heads in bloom can fluctuate greatly depending on environmental conditions and resource availability (Sedgley, 1985; Gaol & Fox, 2002; Yates & Broadhurst, 2002). Pollen release often occurs in the middle of the day when insect abundance is greatest, which likely confers an advantage when it comes to adapting to new habitats in the initial stages of invasion (M.N. Prescott, unpublished data). Where Australian acacias are invasive in Mediterranean-type climate regions, their flowering occurs earlier than, and overlaps with, most native species whose peak flowering occurs in spring (Henderson, 2001; Godoy *et al.*, 2009). Various studies have shown early and extended flowering

phenologies of invasive versus native plants to be correlated with invasive potential (Cadotte & Lovett-Doust, 2001; Pyšek & Richardson, 2007; Pyšek *et al.*, 2009), thus conferring a fitness advantage by reduced competition for pollinators (Stone *et al.*, 1998; Raine *et al.*, 2007). However, while this may be true in general, differences in overall length of flowering period between invasive and non-invasive Australian acacias were found to be non-significant (P. Castro-Díez, unpublished data; see discussion in Castro-Díez *et al.*, 2011).

Peak flowering prior to and during spring, while not unique to invasive Australian acacias, may contribute indirectly to invasiveness in some environments as early and prolonged flowering in *Acacia* species during peak flowering of native species in exotic ecosystems may help mitigate pollen and pollinator limitation. Again, this alone is not likely to contribute to invasiveness but may do so when it is combined with other invasion-enhancing reproductive traits that are not present in non-invasive species.

Breeding system and seed set

Completely self-incompatible species depend entirely on pollinators and mate availability, but self-compatibility and the ability to self-pollinate autonomously assure reproduction against inadequate pollinator visitation and/or mate availability (Eckert *et al.*, 2006). Australian *Acacia* species range from highly self-incompatible to completely self-compatible and autogamous (Table S1) (Moffett, 1956; Bernhardt *et al.*, 1984; Kenrick & Knox, 1989; Morgan *et al.*, 2002), and so probably vary greatly in their dependence on pollinators for realized fecundity. Realized outcrossing rates tend to be high (multi-locus outcrossing rate (t_m) > 0.9 in most species: Table S1) indicating that pollinators do play an important role in their reproduction. Partial self-compatibility and intraspecific variation in self-compatibility seem relatively common in Australian *Acacia* species (Philp & Sherry, 1946; Moffett & Nixon, 1974) with some ability to reproduce by selfing known for six species, five of which are invasive (see Table S1: *Acacia dealbata*, *A. decurrens*, *A. mearnsii*, *A. paradoxa*, *A. saligna*) (J.G. Rodger, unpublished data; George *et al.*, 2008; Millar *et al.*, 2011).

The apparently high prevalence of at least some level of self-compatibility in Australian *Acacia* species is significant given the rarity of uniparental reproduction in woody plants (Barrett *et al.*, 1996). This is consistent with the observation by Rambuda & Johnson (2004) that all 13 woody species investigated in a survey of breeding systems of invasive plants in South Africa were capable of uniparental reproduction. Investigation of Australian *Acacia* species could reveal further details about the evolution of breeding systems and their role in invasiveness in woody species in general. Comparisons between invasive and non-invasive *Acacia* species are hindered by insufficient data here, as elsewhere, but available information suggest that invasive taxa tend to have higher levels of self-compatibility, suggesting ability to self-fertilize may predispose *Acacia* species to invasiveness. However, in shade house trials,

selfed progeny of *A. mearnsii*, *A. decurrens* (Moffett & Nixon, 1974) and *A. dealbata* (J.G. Rodger, unpublished data) have reduced growth and survival, which would erode the reproductive assurance benefits of selfing (Herlihy & Eckert, 2002). Other self-compatible tree species have such high levels of inbreeding depression that it is unlikely that progeny arising from self-pollination ever reach reproductive maturity (Hardner & Potts, 1997; Ishida, 2006; Robertson *et al.*, 2011). A comparison of fixation index for trees from germination to reproduction (e.g. Ishida, 2006) would reveal whether selfed progeny reach reproductive maturity and therefore whether self-compatibility potentially enhances invasiveness.

Even a low capacity for reproduction by self-fertilization could be important in alleviating pollinator and mate limitation, which are likely to occur in the early stages of naturalization and invasion owing to small size or low density of populations (Baker, 1955; Davis *et al.*, 2004). Such factors have been shown to influence seed set in *Acacia* in the native range (Broadhurst & Young, 2006). However, extensive pollen dispersal may maintain outcrossing rates in small patches or isolated plants (Millar *et al.*, 2008, 2011). While ability to self-fertilize may make species more likely to become invasive or to spread at greater rates, it is not essential for invasiveness – there are prominent examples of invasive self-incompatible species in *Acacia* (e.g. *A. auriculiformis*, *A. pycnantha* – see Table S1) and other groups (e.g. Barthell *et al.*, 2001). Our study found no differences in indices of self-compatibility (ISI) nor breeding system strategy (mixed versus outcrossing) between invasive and non-invasive species (Table 1A,B), though data for these traits were extremely limited (see Table S1).

Seed biology

Seed biology seems to be one of the most important factors contributing to the invasion success of Australian acacias (Milton & Hall, 1981; Richardson & Kluge, 2008). Seed biology syndromes in many *Acacia* species are largely shaped by fire-driven ecosystems that are present throughout much of Australia and introduced Mediterranean-type climate regions. Fire-adaptive traits include: production of large quantities of hard-coated, heat-tolerant and long-lived seeds with the capacity for long dormancy; stimulation of germination by heat and/or smoke; seed dispersal and burial by ants; and the ability to resprout (Berg, 1975; Bell *et al.*, 1993; Specht & Specht, 1999), all of which are likely essential for the persistence and invasive success of Australian acacias (see Fig. 4 for photographs of seed biology traits associated with invasiveness).

Dispersal

Dispersal is a crucial aspect of progression from ‘naturalized’ to ‘invasive’ status when recruitment occurs at considerable distances from parent plants (Richardson *et al.*, 2000a,b). Australian acacias possess seed adaptations for dispersal by birds and ants (Davidson & Morton, 1984; O’Dowd & Gill,

1986), although passive dispersal via water, wind and gravity is also common.

Broadly, biotic seed dispersal in *Acacia* falls into two syndromes based on features of arils: a ‘bird-dispersal syndrome’ and an ‘ant-dispersal syndrome’ (O’Dowd & Gill, 1986). The fleshy arillate appendages (in bird-dispersed seeds) and an elaiosome (in ant-dispersed seeds) attach the seed to the seed pod lining and make them accessible to a range of bird and ant species across multiple foraging types. Such generalization of morphological traits associated with dispersal makes limitation of a seed dispersal agent in the introduced range unlikely (see Glyphis *et al.*, 1981; Holmes, 1990a; Richardson *et al.*, 2000a; Underhill & Hofmeyr, 2007). Furthermore, these traits may be evolutionarily labile since *A. ligulata* reportedly displays both syndromes (Davidson & Morton, 1984), each of which has its own advantages. Birds are important agents in that they aid in longer distance dispersal (Holmes, 1990a) and, through ingesting the seeds, are able to aid in the germination of *Acacia* species requiring chemical scarification (e.g. *A. cyclops*, *A. melanoxylon*) (Glyphis *et al.*, 1981; Richardson & Kluge, 2008). Ants rapidly remove and bury *Acacia* seeds in subterranean nests and so contribute to dispersal on a local scale (Holmes, 1990a). Species noted as having a ‘bird-dispersal syndrome’ are likely also dispersed vertically by ants, as myrmecochory accounts for much of the movement of seed from the litter layer into the seed bank (Richardson & Kluge, 2008). Dispersal by birds of an ‘ant-dispersal syndrome’ species appears less likely (O’Dowd & Gill, 1986).

Importantly, seed morphology and dispersal agents in the native range of Australian acacias are not always accurate predictors of dispersal agents in introduced ranges. For example, in Portugal, South Africa and Florida, invasive *Acacia* seeds are effectively dispersed by a wide range of opportunistic agents besides those that one would consider functional equivalents of dispersal agents in the native range. These include baboons, domestic and wild ungulates and humans (Ridley & Moss, 1930; Middlemiss, 1963; Kull & Rangan, 2008). In the Western Cape of South Africa, primarily insectivorous barn swallows ingest seeds and act as effective dispersal agents of *A. cyclops* (Underhill & Hofmeyr, 2007), and other granivorous, ground-dwelling birds disperse *Acacia* seeds (Duckworth & Richardson, 1988; Knight & Macdonald, 1991). In New Zealand, most native avian seed dispersers are now extinct (Anderson *et al.*, 2006), and the ant fauna is relatively depauperate and limited in distribution (Don, 2007), with only three ant species including seeds in their diet. Despite these limitations, at least eight Australian *Acacia* species have become invasive in New Zealand (Richardson & Rejmánek, 2011) with *A. baileyana* showing evidence of long-distance dispersal although the dispersal agent is not known (E.M. Wandrag, unpublished data). Furthermore, in many human-dominated systems, long-distance dispersal of introduced species is mostly human mediated (Trakhtenbrot *et al.*, 2005), so this distinction is likely less important in determining spread rates than may be predicted.

Abiotic dispersal in water and soil is important in many regions (Milton & Hall, 1981). There is a strong association



Figure 4 Important seed biology traits associated with invasiveness in Australian acacias. (a) Seed production of *Acacia saligna* in South Africa during the early 1980s, prior to the introduction of the rust fungus *Uromycladium uromyces*, which has since greatly reduced seed production (photograph: D.M. Richardson). (b) Seed production of *A. longifolia* in its native range in Australia (photograph: C. Harris). Seeds that fall to the ground can remain viable for 50+ years, making their eradication nearly impossible. (c) *A. cyclops* seeds remain in the tree canopy longer than those of species that are typically ant-dispersed; the bright red aril attracts birds that disperse the seeds (photograph: A.M. Rogers). (d) *A. longifolia* seeds are typically ant-dispersed in the native range, although bird-dispersal is predicted based on aril attributes; they are attached to the seed pod by an elaiosome that attracts ants (photograph: C. Harris). (e) Invasive species, such as *A. saligna* pictured here, have a greater tendency to resprout following a disturbance event than non-invasive species (photograph: D.M. Richardson). (f) The mass germination of *Acacia* seeds after fire, as in *A. pycnantha* in South Africa shown here, is a major hurdle to control efforts (photograph: D.M. Richardson).

between *A. dealbata* invasions and watercourses in Chile and Portugal (H. Marchante, unpublished data; Pauchard *et al.*, 2008). Movement of soil for road building is also a major dispersal route of *A. dealbata* and *A. longifolia* in Portugal (H. Marchante, unpublished data). Similarly in South Africa, rivers and soil movement aid in the dispersal of acacias that invade riparian areas, such as *A. mearnsii* (de Wit *et al.*, 2001).

Seed mass in *Acacia* was found to be positively correlated with invasiveness in a recent study (Castro-Díez *et al.*, 2011) but did not consistently differ in our study nor in a multi-species study comparing seed mass between native and introduced ranges (C. Harris *et al.*, unpublished data). These results contradict findings for *Pinus* where smaller seed size is positively associated with invasiveness, as small seeds are more suitable for long-distance dispersal by wind (Richardson, 2006). The difference between pines and acacias in this regard is not surprising. Unlike pines, most acacias are animal dispersed, and dispersal by wind is of trivial importance. Factors other than size contribute to dispersibility, and seed size plays an entirely different role as mediator of colonization and establishment success.

Dispersal traits associated with a bird-dispersed syndrome in Australian acacias clearly predispose these species to spread rapidly in a new environment (see discussion of this for *A. cyclops* in South African fynbos by Higgins *et al.*, 2001)

because of the importance of long-distance dispersal events in driving invasions (Trakhtenbrot *et al.*, 2005). However, of the 23 species of Australian *Acacia* considered invasive (*sensu* Pyšek *et al.*, 2004; Richardson & Rejmánek, 2011), only eight species are known to be bird-dispersed or possess typical bird-dispersed seed traits (Davidson & Morton, 1984; O'Dowd & Gill, 1986; Langeland & Burks, 1998; Stanley & Lill, 2002): *Acacia auriculiformis*, *A. cyclops*, *A. holosericea*, *A. implexa*, *A. longifolia*, *A. mangium*, *A. melanoxylon* and *A. salicina* (see Table S1). Additionally, our analysis found that seed dispersal by birds was not significantly correlated with invasiveness. In Portugal, two of the most invasive and widespread *Acacia* species (*A. dealbata* and *A. longifolia*) are ant-dispersed (Marchante *et al.*, 2010), as are *A. saligna* and *A. mearnsii* in South Africa (French & Major, 2001; Richardson & Kluge, 2008). Thus, the contribution of different dispersal agents to invasiveness remains unclear but further suggests a role of human-mediated dispersal and interactions with environmental factors.

Seed bank dynamics

A reproductive trait that strongly influences invasiveness of Australian acacias is their capacity to form extensive and persistent soil seed banks (Richardson & Kluge, 2008). Accumulation times differ depending on the species (see

Table 2 of Richardson & Kluge, 2008), and the average shortest time frame is roughly eight years. The seeds of some *Acacia* species that have become invasive can remain dormant for 50–100 years or more (Farrell & Ashton, 1978; New, 1984). Richardson & Kluge (2008) list four main factors that contribute to the size of soil-stored seed banks in Australian acacias in South Africa: the annual seed rain; the age of the stand; stand density or canopy cover; and distance from the canopy. Additional factors include level of granivory, decay and germination (Marchante *et al.*, 2010). Biological control agents that negatively affect flower, flower bud or pod production, such as *Melanterius* weevils (Dennill & Donnelly, 1991; Impson *et al.*, 2004) that directly feed on acacia seeds, can reduce annual seed rain. The rate of seed accumulation in the soil increases until the stand is about 30 years old, and denser stands produce more seeds, so control efforts to reduce seed production should focus on younger, denser *Acacia* stands (Milton & Hall, 1981; Holmes, 1990b). Seed density in the soil is highest under the tree canopy and decreases sharply with distance (see Zenni *et al.*, 2009; Marchante *et al.*, 2010), although Marchante *et al.* (2010) found a few seeds of *A. longifolia* up to 7 m from the edge of invaded stands.

The main drivers of seed bank persistence and maintenance appear to be ants, although gravity and water may be the dominant drivers where ants are absent. Once seeds have dropped to the ground, ants bury many of them in their nests to allow them to exploit arils (Milton & Hall, 1981). In doing so, they often account for the majority of vertical seed movement into the upper seed bank. *Acacia* seeds gain a threefold advantage through protection from above-ground seed predators, protection from fire and incorporation into the seed bank (Gill, 1985; Holmes, 1990a). In South Africa, ants may play a critical role in accumulating seed banks of Australian acacias and aiding in their invasiveness (Holmes, 1990c; Richardson *et al.*, 2000a).

The role of seed bank density in *Acacia* invasiveness is unclear. Both higher and lower seed bank densities have been recorded in the introduced range of various *Acacia* species when compared to that in the native range (Milton & Hall, 1981; Richardson & Kluge, 2008; Marchante *et al.*, 2010). Additionally, methods of measuring seed bank and seed rain vary widely, making comparisons between introduced and native ranges problematic (see Table 2 for a summary of Australian *Acacia* seed data from various introduced and native regions). Prolific seed production and large accumulations of seeds in the seed bank certainly contribute to a species' ability to invade an ecosystem but these qualities alone do not guarantee invasiveness. Buist (2003) found that closely related pairs of rare and widespread *Acacia* species produced similar numbers of seeds and similar-sized, persistent soil seed reserves, indicating that level of seed production does not necessarily determine abundance of a species. These traits likely need to work in concert with certain physiological and morphological traits, such as germination ability, resource utilization, rapid growth of seedlings and dispersal investment, to contribute to invasiveness.

Germination

The majority of invasive *Acacia* species possess seeds whose germination is stimulated by fire, but some invasive species, notably bird-dispersed taxa, may be stimulated to germinate through chemical scarification via ingestion by an appropriate dispersal agent (Glyphis *et al.*, 1981; Fraser, 1990; Richardson & Kluge, 2008). These stimuli are required to break physical dormancy of the hard, water impermeable seed coat and allow germination of *Acacia* seeds, which have consistently high viability and low germinability over time. However, in Portugal, total viability and germinability were found to be significantly higher (and dormancy lower) in seeds from recently invaded soils for *A. longifolia* (Marchante *et al.*, 2010).

Invasive Australian acacias tend to germinate after disturbance, although disturbance is not essential. *Acacia dealbata* shows high survival within native forest and in open areas in Chile where it can endure long periods of drought and shade under canopies of native trees (Fuentes-Ramírez *et al.*, 2011). Moreover, mutualistic relationships with nitrogen-fixing bacteria are important for successful establishment of leguminous species, so the presence of compatible rhizobia is also essential for determining the colonization ability of introduced species (Parker *et al.*, 2006; Rodríguez-Echeverría *et al.*, 2011). Interestingly, Rodríguez-Echeverría *et al.* (2011) found that these bacterial symbionts are often cointroduced with their *Acacia* hosts from Australia, suggesting the presence of suitable soil symbionts in the introduced range may not be an important limiting factor in *Acacia* invasions *per se*.

Studies from the introduced ranges of Australian acacias report that a considerable number of seeds produced and allocated to seed rain are lost to factors such as early germination, granivory or decay (Marchante *et al.*, 2010). However, the consistently high seed viability found in many species of *Acacia* appears to be fundamental to their ability to invade (see Table 2) (Richardson & Kluge, 2008; Marchante *et al.*, 2010). Germination characters *per se* do not appear to be characteristic of invasiveness as invasive Australian *Acacia* species in South Africa can show opposing characteristics of either high dormancy, low germination and decay rates and rapid seed bank accumulation, or low dormancy, high germination and decay rates and gradual seed bank accumulation (Richardson & Kluge, 2008).

Comparisons of rare and widespread species show some association with factors that influence seed germination. The burial depth and heat-stimulation requirements of a species are important factors affecting germination that can determine how rare or widespread it is (Brown *et al.*, 2003). Comparisons of reproductive traits in two rare acacias and their common relatives showed differences in the germination (reduced range of temperature for germination in rare species) and higher rates of predation of fruit and seed in the rare species (Buist, 2003). Seed viability and dormancy levels between invasive and non-invasive species have not been compared. It may be predicted that, because such traits are adaptations to

Table 2 Seed rain density (SRD), seed bank density (SBD) and seed viability (SV) for Australian acacias in native and introduced ranges.

<i>Acacia</i> species	Seed rain density per m ² per year (SRD)	Seed bank density per m ² (SBD)	Seed viability (SV)	Region	References	Observations
<i>A. baileyana</i>	19559	–	–	Australia (native range)	17	SRD – maximum #seed/tree
<i>A. baileyana</i>	1824 (3010)	–	–	New Zealand	26	SRD – average # seeds per m ² averaged over 7-day period
<i>A. cyclops</i>	–	1430–5140 (142–281)	46–95.3%	South Africa	10	
<i>A. cyclops</i>	–	2832–7792 (402–1019)	99.2%	South Africa	8	SBD – range of four different blocks
<i>A. cyclops</i>	1197 [1373–3019*]	2031	87%	South Africa	15	SRD – *estimated #seed per m ² projected canopy
<i>A. cyclops</i>	540 (710)	–	–	Australia (introduced range)	6	SRD – estimated from reproductive output data (determined by dividing total mass of seeds removed from pods by mass per individual seed)
<i>A. cyclops</i>	1900 (1930)	–	–	Australia (native range)	6	
<i>A. dealbata</i>	–	10000	90%	Chile	25	
<i>A. dealbata</i>	2553 (3244)	–	–	New Zealand	26	SRD – average # seeds per m ² averaged over 7-day period
<i>A. dealbata</i>	–	ca. 22500	30%	Portugal	13	SV: probably underestimated (seeds heated to 50°C without scarification)
<i>A. elata</i>	–	–	50%	–	22	SV – final germination after scarification
<i>A. holosericea</i>	–	–	>95%	Australia (native range)	7	
<i>A. longifolia</i>	2000–12000	500–1500	>85%	Portugal	14	SRD – 2000: smaller trees next to the ocean (windward); 12000: bigger trees leeward
<i>A. longifolia</i>	–	–	>88%	Portugal	16	
<i>A. longifolia</i>	11500	34000	–	South Africa	19	SRD – maximum number
<i>A. longifolia</i>	–	2078–3473 (488–498)	99%	South Africa	21	
<i>A. longifolia</i>	2923	7646	97%	South Africa	15	
<i>A. longifolia</i>	–	4528 (1075)	99%	South Africa	4	After introduction of biological control agent, max numbers
<i>A. longifolia</i>	2530 (3430)	–	–	Australia (introduced range)	6	SRD – estimated from reproductive output data (determined by dividing total mass of seeds removed from pods by mass per individual seed)
<i>A. longifolia</i>	810 (1180)	–	–	Australia (native range)	6	
<i>A. mangium</i>	410	–	–	Indonesia	23	SRD – estimated from seed production in kg per ha per year
<i>A. mearnsii</i>	–	5314/696	–	South Africa	20	SBD- maximum number/average

Table 2 Continued.

<i>Acacia</i> species	Seed rain density per m ² per year (SRD)	Seed bank density per m ² (SBD)	Seed viability (SV)	Region	References	Observations
<i>A. mearnsii</i>	–	38340	–	South Africa	15	
<i>A. mearnsii</i>	–	–	>83.4%	South Africa	12	
<i>A. melanoxylon</i>	3218	48739	70%	South Africa	15	SRD & SBD: Donald, 1959 cited by Milton & Hall, 1981
<i>A. melanoxylon</i>	–	–	85–91%	Australia (native range)	2	
<i>A. melanoxylon</i>	740 (800)	–	–	Australia (introduced range)	6	SRD – estimated from reproductive output data (determined by dividing total mass of seeds removed from pods by mass per individual seed)
<i>A. melanoxylon</i>	1160 (1810)	–	–	Australia (native range)	6	
<i>A. paradoxa</i>	–	1000	–	South Africa	28	
<i>A. paradoxa</i>	58#	–	–	Australia (native range)	1	SRD – #firm seed production per plant
<i>A. pycnantha</i>	31#	–	99%	Australia (native range)	1	
<i>A. saligna</i>	–	7920–45800 (560–3220)	>86%	South Africa	10	
<i>A. saligna</i>	2645–13472	–	–	South Africa	27	SRD – measured in 1989, <i>ca.</i> 2 years after introduction of biocontrol agent
<i>A. saligna</i>	446–3035	–	–	South Africa	27	SRD – measured in 2004, <i>ca.</i> 18 years after introduction of biocontrol agent
<i>A. saligna</i>	5443 [10562*]	11920	83%	South Africa	15	SRD – #seed/tree based on few trees; * estimated seed per m ² projected canopy
<i>A. saligna</i>	–	715–8097	–	South Africa	9	SBD – after introduction of biological control agent; values estimated from 4 places and 3 depths
<i>A. saligna</i>	–	–	>90%	Israel	3	
<i>A. saligna</i>	–	2000–189000 (53333)	–	South Africa	18	After introduction of biological control agent; average from 8 sites, samplings during 6 years
<i>A. saligna</i>	–	1389–3600 (207–279)	–	Australia, New South Wales (introduced range)	24	
<i>A. saligna</i>	–	–	73%	–	22	SV – final germination after scarification
<i>A. saligna</i>	–	3158–38714 (1194–4006)	>65%	South Africa	11	SBD – range of 4 sites, at 0–15 cm
<i>A. saligna</i>	760 (750)	–	–	Australia (introduced range)	6	SRD – estimated from reproductive output data (determined by dividing total mass of seeds removed from pods by mass per individual seed)
<i>A. saligna</i>	540 (650)	–	–	Australia (native range)	6	

Table 2 Continued.

<i>Acacia</i> species	Seed rain density per m ² per year (SRD)	Seed bank density per m ² (SBD)	Seed viability (SV)	Region	References	Observations
<i>A. salicina</i>	–	–	77%	–	22	SV – final germination after scarification
<i>A. victoriae</i>	–	50–3900	80%	Australia (native range)	5	

Values refer to mean values unless otherwise specified (standard deviation in parentheses where available).

1: Brown *et al.* (2003); 2: Burrows *et al.* (2009); 3: Cohen *et al.* (2008); 4: Fourie (2008); 5: Grice & Westoby (1987); 6: C. Harris *et al.* (unpublished data); 7: Hellum (1990); 8: Holmes (1989); 9: Holmes (2002); 10: Holmes *et al.* (1987); 11: Jasson (2005); 12: Kulkarni *et al.* (2007); 13: H. Marchante, unpublished data; 14: Marchante *et al.* (2010); 15: Milton & Hall (1981); 16: M. Morais, unpublished data; 17: Morgan (2003); 18: Morris (1997); 19: Pieterse (1987); 20: Pieterse (1997); 21: Pieterse & Cairns (1986); 22: Rehman *et al.* (2000); 23: Saharjo & Watanabe (2000); 24: Tozer (1998); 25: G. Valencia, unpublished data; 26: E.M. Wandrag, unpublished data; 27: Wood & Morris (2007); 28: Zenni *et al.* (2009).

fire-driven ecosystems, other *Acacia* species originating from similar regions also likely possess such germination traits.

Alternative modes of reproduction and persistence

Acacia displays a variety of regeneration strategies besides germination from seed, including root suckering, and basal resprouting (Bell *et al.*, 1993; Reid & Murphy, 2008), which predispose them to weediness and can occur following disturbance such as fire and mechanical removal (Reid & Murphy, 2006). In South Africa, for example, species such as *A. cyclops*, which lack the ability to resprout after fire, have high demographic dependence on seeds, while species such as *A. saligna*, which resprouts vigorously, depend less on seeds for population persistence. Spooner (2005) found that disturbance by road works in Australia triggered a range of responses, such as a combination of basal resprouting, root suckering and seedling emergence, which led to a population increase for three *Acacia* species. Similarly, resprouting is a major reproductive mechanism in *A. dealbata* in Chile and Europe and may facilitate its rapid invasion of new environments (Marchante *et al.*, 2008; Lorenzo *et al.*, 2010; Fuentes-Ramírez *et al.*, 2011). Our study also found that resprout ability was greater for invasive species than for non-invasive species where they are introduced globally. Long-lived seed banks and ability to resprout are key determinants of persistence; together with the ability to disperse, these traits are hugely influential ingredients of invasive success since they ensure persistence and effectively permanent occupancy of invaded sites (e.g. Richardson & Cowling, 1992).

DISCUSSION

Our literature review found that traits including generalist pollination systems, prolific seed production, efficient seed dispersal and the accumulation of large and persistent seed banks, which often have fire-, heat- or disturbance-triggered germination cues, are characteristic of Australian acacias in general. We did not find distinct reproductive syndromes that differed between invasive and non-invasive species, although

this may be both because trait data were not available for all species, and those species for which data are available might not be representative.

Pollinator-mediated seed production is likely to facilitate invasion of *Acacia* species where they are introduced but should not differ for introduced non-invasive species as Australian acacias possess similar floral morphology and attract similar (generalist) pollinator groups (e.g. *Apis mellifera*). Flowering and seed production are clearly important for invasion success and account for the massive number of propagules that accumulate to create a long-lived soil seed bank that is the largest hurdle to effective control (Wilson *et al.*, 2011). We found that invasive species reach reproductive maturity earlier, and this could certainly contribute to a faster accumulation of a seed bank, which is a vital requirement for ensuring persistence in regularly disturbed environments, such as those in which most Australian acacias are invasive (Richardson *et al.*, 1990, p. 362). These results are supported in other studies that have also documented the important role of a short juvenile interval to seed production (in *A. baileyana*, see Morgan *et al.*, 2002) and spread rate (in *Pinus*, see Higgins *et al.*, 1996; Higgins & Richardson, 1999). Time to reproductive maturity was also found to be shorter for invasive than non-invasive species when phylogeny was accounted for. This trait has not been discovered to have phylogenetic signal, and in an analysis using the most recent phylogeny for Australian *Acacia*, Miller *et al.* (2011) found that invasive species were phylogenetically over-dispersed (i.e. there was no phylogenetic signal for invasiveness). However, our results suggest that certain traits, which may be related to evolutionary history, can affect invasiveness and indicate that phenological precocity may be important for future consideration in phylogenetic studies.

Seed dispersal is critical for the spread of introduced Australian acacias, and although biotic dispersal agents are important, the majority of dispersal is likely human-mediated and focussed on economically important species. The ability to resprout undoubtedly aids in persistence during initial establishment as it makes a population less susceptible to stochastic events. This is supported by the results of our study that show

resprout ability to be significantly greater for invasive species. Our results are similar to those of Pyšek & Richardson (2007) who found that vegetative reproduction is positively associated with invasiveness in vascular plants across multiple comparative studies. However, resprouting ability should not directly aid in the ability of plants to spread.

There is much room to improve our knowledge of the reproductive biology in this genus. The role of pollinator-mediated seed production, especially by *Apis mellifera*, appears to be important to reproductive success of *Acacia* where they are introduced, and this needs to be formally tested. In addition, self-compatibility has the potential to facilitate the invasion process by enabling seed production when mate and pollinator availability is low, but formal tests are needed to see whether effects of inbreeding depression cancel out such benefits. Whether the reproductive traits that we tested are related to evolutionary history is unknowable at this point. The lack of clear phylogenetic signal in *Acacia* is probably due to the lack of data both in the value of the reproductive traits and in the sampling of the phylogenetic tree. That our results suggest reproductive traits are related to evolutionary history is an important issue that will need further research. Thus, we recommend that future analyses incorporate variable and phylogenetic data for a wider array of invasive and non-invasive species (see Box 1 for a list of research priorities).

The finding that certain reproductive traits show no obvious correlation with invasiveness in Australian acacias may be attributable to a number of factors. First and foremost is the shortage of data for many Australian acacias, both invasive and non-invasive, and consequent small sample sizes (see Table 1-A,B for sample sizes). This makes detection of more subtle correlations between reproductive traits and invasiveness difficult, resulting in an incomplete picture for understanding such relationships. Secondly, there is clearly no single 'ideal' reproductive syndrome that equips certain species in this group particularly well to establish, undergo rapid population

growth (often from small founder populations), and to persist across the full range of habitats to which they have been introduced. Thirdly, if much of the reproductive trait data for invasive and non-invasive introduced species comes from studies within the native range, they may not incorporate differences in measurements because of region-specific factors of the introduced range. Such disparities in data highlight the need for measuring reproductive performance of individual invasive *Acacia* species in the introduced and native range. A fourth possibility is that all Australian acacias possess inherent reproductive and/or other life-history traits that facilitate invasiveness, and thus, all Australian acacias have the capacity to become invasive. Specific features of reproductive biology may be less important than a range of human-mediated factors that influence the abundance and distribution of species across potentially invulnerable sites, such as facets of the introduction history, propagule pressure, residence time and country-specific utilization or treatment of particular species via economic, environmental and social avenues.

Key stages for invasiveness of the reproductive life cycle of Australian acacias are useful to identify to determine options for the intervention to reduce success and achieve management objectives (Wilson *et al.*, 2011). Control efforts should aim, in the first instance, to prevent the accumulation of massive seed banks (Richardson & Kluge, 2008) as once a seed bank is established, the population is practically impossible to eradicate. Biological control provides the most cost efficient, long-term control method and should be the foundation of effective integrated control operations. The upper seed bank is where the majority of *Acacia* seeds are able to successfully germinate and so should be the target area for control measures of which burning is the most effective. However, the applicability in practice of such useful additional measures as burning, mechanical control and herbicide application is context specific. To reduce human-mediated dispersal, planting Australian acacias near points of dispersal pathways (e.g. near

Box 1 Priorities for future research on the reproductive ecology of Australian acacias

To elucidate determinants of invasiveness, a variety of approaches are necessary to establish a complete profile for identifying reproductive traits consistently associated with invasion success in novel environments. This includes conducting multi-species studies encompassing native and multiple introduced ranges and comparative studies that contrast invasive *Acacia* species with co-occurring native species, as well as with non-invasive *Acacia* species or closely related taxa. Data for these comparisons regarding reproductive traits are widely lacking, and further studies are needed to gather information on reproductive biology.

Very little research has been carried out on the pollination biology of Australian acacias. Given its fundamental role in reproductive success and therefore invasion, further research is needed to determine the relative contributions of different insect visitors and wind pollination to outcrossing and seed set in the introduced range for invasive species and non-invasive species as well as for invasive species in exotic and native ranges. This information could be used to determine whether pollination efficiency contributes to a species' invasiveness.

Both breeding system data, based on controlled pollinations that indicate potential for selfing, and mating system data, based on molecular markers that give the rates of outcrossing, are needed. Breeding system data are lacking for some invasive *Acacia* species and for almost all non-invasive species in their introduced ranges. Comparisons are needed between both groups to determine how breeding system links to invasiveness and also between invasive species in the native range and in the introduced range to examine the extent of interspecific breeding system plasticity. Findings have implications for management protocols regarding genetic modifications and expected seed yields following self-pollination.

Thorough documentation of seed dispersal syndromes in the group is needed, for example, to determine whether the bird-dispersal syndrome is overrepresented in taxa that have become invasive. Insights from such work will provide useful information for improving the management of already invasive Australian acacias and help to refine tools for more effective screening of new introductions.

rivers, along roads) should be prohibited (Wilson *et al.*, 2011). Although the significant association of resprouting ability with invasiveness in the phylogeny-free analyses may be misleading in evolutionary terms, it is still useful from a management perspective. Thus, wherever Australian *Acacia* species that attain reproductive maturity early or have a strong capacity for resprouting are planted, proactive measures should be implemented to manage invasiveness.

Despite our attempts to test for individual reproductive traits that contribute to invasiveness, larger sample sizes facilitated by greater data availability are necessary before any firm conclusions can be drawn in this regard. Because there is still a depauperate knowledge surrounding this group of globally important invasive plants, reproductive traits of invasive Australian acacias and their distinguishing characteristics need to be the focus of future research directives (see Box 1). Hence, until there is substantial evidence to the contrary, caution should be exercised concerning introductions of all Australian acacias given their general ability to reproduce effectively in new locations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 The complete set of reproductive traits for introduced Australian acacias ($n = 126$).

Table S2 The complete set of reproductive traits for non-introduced Australian acacias ($n = 324$).

Table S3 List of Australian *Acacia* flower visitors.

Appendix S1 Accession numbers for those species used in phylogenetic analyses.

Appendix S2 Phylogeny-free analyses of relationships between individual reproductive traits in Australian *Acacia* species and invasive status (invasive versus non-invasive).

Appendix S3 The effect of individual reproductive traits on Australian *Acacia* species' invasive status (invasive versus non-invasive) using phylogeny as a covariate.

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BIOSKETCH

All co-authors are actively involved in research on the ecology of Australian *Acacia* species. **M. G. is a Master's** student and S.D.J., J.J.L.R., D.M.R. and J.R.U.W. are core team members at the DST-NRF Centre of Excellence for Invasion Biology (<http://academic.sun.ac.za/cib/>). M.G.'s thesis at Stellenbosch University deals with the effects of *Acacia saligna* on native plant–pollinator communities. Her research interests lie in invasion biology, novel ecosystem interactions and restoration and conservation research.

Author contributions: M.R.G. and D.M.R. conceived the ideas; M.R.G., E.M. and H.M. collected most of the new data; M.B., N.G., M.R.G., C.H., E.M., H.M., J.T.M., D.J.M., M.N.P., J.G.R. and E.M.W. contributed additional data; J.J.L.R., J.T.M. and G.N.S. wrote the phylogenetic methods section; J.J.L.R. and J.T.M. reconstructed the phylogeny; M.R.G. and J.R.U.W. analysed the data; E.M. and H.M. created Table 2; J.G.R. and G.N.S. contributed to the 'Pollination biology' section; M.B., S.D.J. and J.G.R. contributed to the 'Breeding system' section; A.F.-R. contributed to 'Germination' section; A.P. provided conceptual insight and revision support. M.R.G. led the writing with support from D.M.R.

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APPENDIX 1

Description of variables, abbreviations and levels used in statistical analyses and Table S1. T = True, F = False, NA = not applicable.

Variable type	Abbreviation	No. species for which data are available	Levels (and range of values if continuous)	References
<i>Explanatory</i>				
Reproductive trait				
Age to reproductive maturity	Mature	39	Categorical, binary: '1' \leq 2 years; '2' \geq 2 years	1–6
Multi-locus outcrossing rate (t_m)	Outcross	8	Continuous: 0.65–0.97	7–15
Index of self-incompatibility (ISI) (infructescence per inflorescence)	Compatible1	9	Continuous: 0.02–0.96	16–19
ISI (pods per inflorescence)	Compatible2	10	Continuous: 0.008–1.1	16;17;19;20
Breeding system*	Breed	13	Categorical: 'apomictic'; 'SI' = self-incompatible; 'pSC' = partially self-compatible; 'SC' = self-compatible	9; 12; 16; 17; 19–22
Combined measure of breeding system†	Combined	13	Categorical, binary: 'Mixed' or 'Outcross'	see footnote †
Seed dispersed by ants	Ant	16	Categorical: T/NA‡	5; 20; 23–25; 26
Seed dispersed by birds	Bird	13	Categorical: T/NA	6; 23; 24; 26–30
Biotic seed dispersal	Dispers (combination of previous two columns in Table S1)	27	Categorical, binary: 'not bird' dispersed if ant = T & bird = NA; 'bird' dispersed if bird = T	
Seed mass	Seed mass	122	Continuous: 2.72–219.77 (mg)	1; 24; 31
Resprout ability	Resprout	75	Categorical, binary: T/F	5; 31; 32
Duration of flowering season	Flower duration	81	Continuous: 2–12 (months)	5; 31–33
<i>Response</i>				
Invasive or not invasive	Invasive		Binary: 0/1	34

1: J.T. Miller, unpublished data; 2: Australian Native Plants Society, <http://anpsa.org.au/a-pod.html>, October 2010; 3: Global Invasive Species Database, <http://interface.creative.auckland.ac.nz/database/species/ecology.asp?si=1662&fr=1&sts=sss&lang=EN>, 1 October 2010; 4: Kerala Agricultural University, 2002; 5: World Wide Wattle, <http://www.worldwidewattle.com>, February 2011; 6: Zenni *et al.* (2009); 7: Broadhurst *et al.* (2008); 8: Butcher *et al.* (1999); 9: George *et al.* (2008); 10: Millar *et al.* (2008); 11: Moffett (1956); 12: Moran *et al.* (1989b); 13: Muona *et al.* (1991); 14: Philp & Sherry (1946); 15: Coates *et al.* (2006); 16: M. R. Gibson, unpublished data; 17: Kenrick & Knox (1989); 18: Moncur *et al.* (1991); 19: J. G. Rodger, unpublished data; 20: Morgan *et al.* (2002); 21: Andrew *et al.* (2003); 22: Moffett & Nixon (1974); 23: Davidson & Morton (1984); 24: Kew Gardens Seed Information Database, <http://data.kew.org/sid/sidsearch.html>, February 2011; 25: Lorenzo *et al.* (2010); 26: O'Dowd & Gill (1986); 27: Langeland & Burks (1998); 28: Moran *et al.* (1989a); 29: Stanley & Lill (2002); 30: Starr *et al.* (2003); 31: Castro-Díez *et al.* (2011); 32: D. J. Murphy, unpublished data; 33: Arbres et arbustes de La Réunion, http://arbres-reunion.cirad.fr/especes/fabaceae/acacia_heterophylla_willd, February 2011; 34: Richardson & Rejmánek (2011).

*When only t_m was available, we used the criteria: SI is $t_m \geq 0.8$.

†Inference from t_m , ISI and breeding system for which species are classified as either outcrossing (if $t_m \geq 0.8$ or ISI ≤ 0.5 a species is classified as outcrossing) and otherwise as mixed mating.

‡References could only confirm (and not refute) that an ant or bird dispersed seed of a given species, and thus, criteria for 'not bird' dispersed were required (see Biotic seed dispersal (above) and Methods section of main article).